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Modeling Regeneration of Douglas fir forests in Central Europe

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Abstract

Modeling regeneration and growth of juvenile trees is highly relevant for simulating the growth behaviour of forest stands, which permits evaluating forest management options for climate change adaption. An important adaptation option is tree species selection. Douglas fir, a non-native tree species from north western America, was introduced in many Central-European countries and is now one of the most frequent non-native tree species in Europe. In this study, we develop a regeneration tool to predict the regeneration establishment and juvenile tree height growth of Douglas fir in central Europe. We implement this regeneration tool in the tree growth simulator MOSES and test the potential invasiveness using data from 28 Douglas fir dominated stands with natural regeneration located in Austria and southern Germany. Our results suggest that regeneration establishment and juvenile tree growth is driven by overstory competition as well as edge effected incidence of light. Douglas fir re-

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generation shows no invasive behaviour, but in contrast requires forest management to survive.

1. Introduction

Douglas fir (*Pseudotsuga menziesii* (*Mirb.*)) is an important non-native tree species in Europe and has become of increasing interest as an adaptation option to climate change. It is also considered as a potential alternative to Norway spruce (*Picea abies L. Karst*) for low elevations (Lavender and Hermann, 2014) because of its enhanced drought resistance and excellent growth behaviour (Eilmann and Rigling, 2012; Pharis and Ferrell, 1966).

Within its native distribution range in western North America, two distinct varieties of Douglas fir are known: (i) the coastal variety (*P. menziesii* var. *menziesii*) and the (ii) interior variety (*P. menziesii* var. *glauca*). The coastal variety grows along the coast and the west phasing slopes of the Rocky Mountain range from British Columbia, Canada to California, USA. The interior variety (also called Rocky-Mountain variety) grows further east from British Columbia across the Rocky Mountains to New Mexico (USA) (Eckenwalder, 2009).

The distribution of Douglas fir fir in Europe is the result of a long introduction history, which started in 1826 (Köble and Seufert, 2001). In Austria the share of Douglas fir on the total growing stock is about 0.2%, and covers about 10.000 ha (ÖWI, 2016). The Douglas fir forests are located mainly in the Eastern part of Austria. According to the Austrian National Forest Inventory, the area of Douglas fir has doubled since 2002 (Gabler and Schadauer, 2008). In Germany 2% of the growing stock are Doulas fir and the spieces covers about 218.000 ha (BMEL, 2014).

While for the Douglas fir plantations established after the 1960 the seed origin is known, the old Douglas stands established prior to the 1960, are of unknown origin. These stands have existed longer than one rotation cycle and produce abundant natural regeneration, which could be referred to as the "second generation". Hintsteiner et al. (2018) showed, that most of these old Douglas fir stands originate from the recommended areas in North America (mainly from the provenances Ashford Elbe and Snoqualmie River, which are located in the North Cascades from the US state of Washington, in the north of the river Columbia).

Successful forest management requires information about the regeneration dynamics of forests and how this may be implemented in existing growth models. In principle two types of growth models are in place: (1) yield tables, which assess the mean stand development and (2) tree growth models which predict the individual tree growth according to age, competition and site conditions. A typical example is

tree growth model MOSES – Modeling stand response (Hasenauer, 2006; Klopf, 2014; Thurnher et al., 2017). MOSES is parametrized for several important European tree species including Douglas fir (Mayer, 2014), but lacks a regeneration tool for Douglas fir.

Regeneration predictions are commonly based on (1) the establishment of regeneration and (2) the juvenile growth and tree mortality (Biber and Herling, 2002; Golser and Hasenauer, 1997; Hasenauer and Kindermann, 2006; Hynynen et al., 2002; Schweiger and Sterba, 1997). A regeneration model consists of several equations which predict the number of juveniles by species, the survival, and height growth of new established trees. Note that although damage to seedling establishment and regeneration growth due to browsing, timber harvesting, etc. should be taken into account, relatively little information is available for Douglas fir.

Forest regeneration tends to be sporadic, i.e. little or no regeneration for some years and large amounts in those years when it does occur. Thus a two-stage approach of regeneration modeling is commonly applied (Ferguson et al., 1986; Ferguson and Carlson, 1993; Miina and Saksa, 2006; Schweiger and Sterba, 1997; Solomon and Leak, 2002), where first, the probability of regeneration on a given plot is predicted and then the juvenile tree growth is predicted.

The objectives of this study are (1) to apply the regeneration approach suggested by Hasenauer (1994) for Douglas fir forests in central Europe, (2) to evaluate the model results and (3) to implement them into the tree growth model MOSES and analyse the invasiveness of Douglas fir.

2. Methods

The estimation of the probability of regeneration follows the approach suggested by (Kindermann, 2004), (Hasenauer and Kindermann, 2006) and is a generalized linear model (GLM):

$$p = \frac{1}{1 + e^{-a \cdot x}} \tag{1}$$

Where p is the probability of regeneration, a, are the coefficient estimates of the vector x covering the independent variables konk, a measure for competition, dbh_{max} , the maximum diameter at breast height by tree species in the overstory of a sample plot, and Hum the humus type. The competition index konk includes both the competition

in overstory as well as within regeneration layer:

$$konk = \frac{\sum ((a*mdbh)^b \cdot n_{rep} \cdot c)}{10000}$$
 (2)

 n_{rep} is the number of stems per ha represented by each tree within a sample plot. For example, the blow-up factor for a fixed sample area of 16 m² is 625 (10.000/16=625). mdbh is a proxy for the crown area of a tree. For trees ≤ 1.3 m in height the mdbh is set to the height of the tree in meters and for taller trees mdbh is calculated by its dbh in cm plus 1.3. a, b, c are species specific coefficients according to Kindermann (2004) and are calculated iteratively until the plots with and without regeneration can be differentiated. Coefficients a, b, c for Norway spruce and Common beech have been taken from Kindermann (2004).

The density regeneration approach by tree species (N_{BA}) is equal to the regeneration model (see equation 1) and incorporates the same independent variables, konk, db- h_{max} and Hum. The only difference is that a Poisson algorithm is used for estimating the coefficients:

$$N_{BA} = e^{a \cdot x} \tag{3}$$

With a the coefficient estimates of the vector x, which consists of the variables konk, dbhmax, Hum. Equation (3) is only applied if regeneration establishment is predicted.

Predictions of the height growth of juvenile trees are based on the potential modifier approach (see Golser and Hasenauer 1997), where in a first step (i) the 5-year height increment potential of a given tree is derived from site index functions. In a second step (ii) this potential height increment is reduced to actual height growth applying two reduction factors, Overstory competition expressed as the *CCF*, and the competition within the regeneration itself, which is derived as the sum of the trees taller than the subject tree. The compensation factor *SUMD* addresses potential compensation effects in height growth due to the edge effected incidence of light. The equation has the following form (Golser and Hasenauer 1997):

$$ih = ih_{pot} \cdot \left(1 - e^{\frac{-1}{a \cdot CCF + b \cdot nTaller} + c \cdot SUMD}\right) \tag{4}$$

Where ih is the 5-year height increment, ih_{pot} is the potential 5-year height increment derived from site index functions, *CCF* the Crown Competition Factor according to Krajicek et al. (1961), N_{Taller} the number of trees taller than the subject tree, and *SUMD*

the compensation factor of edge effected incidence of light.

The calculation of ih_{pot} (the potential 5 year height increment) requires the selection of a site index (*SI*) function. We used the height curve from Mitscherlich/Richards (see Kindermann and Hasenauer, 2005; Thurnher et al., 2017), which determines the top height of a tree according to stand age, site index and species specific coefficients. These coefficients have been taken from Kindermann and Hasenauer (2005), who calibrated the height curve for all main tree species in central Europe, including Douglas fir. Since we wanted to employ the dominant height development of Douglas fir with data from Eckmüllner (2015), we re-calibrated the function. The dominant tree height needed for the definition of site index (SI) was derived according to Pollanschütz (1975). Missing tree heights of the sampling data were derived according to Peterson (1985).

The crown competition factor *CCF* was calculated according to Krajicek et al. (1961) with coefficients for open grown trees from Hasenauer (1997).

SUMD, the incidence of light, is a compensation factor for the two described competition measures CCF and N_{Taller} , and is quantified by the weighted sum of distances (SUM of Distances) according to Golser and Hasenauer (1997):

$$SUMD = \left(\sum_{n=1}^{N_d} \frac{1}{DIST_i} \cdot \frac{2DH}{N_d}\right) - 1 \tag{5}$$

Where N_d is the number of directions, *DIST* the distance to the stand edge, and *DH* the dominant height of the stand.

3. Data

We obtained 28 Douglas fir stands with natural regeneration growing in Austria and Germany. The plots with a minimum area of 0.25 ha cover a wide range of bioclimatic regions (latitude between 47.5°N and 49.0°N, longitude between 8.6°E and 16.4°E). The share in the basal area of Douglas fir had to be > 75% to be selected. The data collection followed a hierarchical structure including three layers, (1) the overstory with trees > 10 cm in dbh, (2) an intermediate layer covering trees > 1.3 m in h but \leq 10 cm in dbh, and (3) the regeneration layer ($h \leq$ 1.3 m).

Overstory data were collected at a fixed sample plot with a radius of 20 m. Trees species, dbh, horizontal distance to the plot centre, and azimuth was recorded. Tree height and heights to life crown was recorded. The same information was collected on four subplots representing the intermediate layer. Stand age was determined from increment cores. The summary statistics of the overstory data are given in Table 1.

Table 1: Summary statistics of the 28 Douglas fir stands. Elev is elevation, Temp is mean annual temperature, Precip is mean annual precipitation, N/ha is stem number per ha, BA is basal area, V is stem volume, DH is dominant height, CCF is Crown Competition Factor, SI is site index as dominant height at age 100.

	Site-c	haracteri	stics	Stand	Stand-characteristics							
Plot	Elev	Temp	Precip	Age	N/ha	BA/ha	V/ha	DH	CCF	SI		
Nr.	(m)	(°C)	(mm)			(m ²)	(m³)	(m)	(%)			
1	290	9.9	600	90	136	24	324	35	135	35		
2	460	9.6	720	84	164	42	720	43	308	46		
3	560	9.1	790	82	211	43	721	43	368	47		
4	520	9.3	770	40	399	28	278	22	360	42		
5 6	360	9.5	650	38	558	36	371	25	573	49		
	370	9.1	570	52	188	20	223	27	142	40		
7	400	9	580	108	61	17	219	33	77	30		
8	430	9.1	640	58	748	61	822	33	906	47		
9	440	8.9	620	43	306	35	474	31	413	57		
10	410	9	610	42	285	32	386	29	237	53		
11	330	9.4	960	70	165	41	595	39	340	47		
12	530	7.9	710	121	247	55	863	40	568	36		
13	820	7.1	2100	110	160	65	1317	54	407	50		
14	640	8	900	109	76	38	740	51	279	48		
15	660	7.9	910	105	108	41	829	54	378	50		
16	590	8.3	890	104	207	42	821	51	263	48		
17	660	8.1	1110	54	324	52	650	33	483	49		
18	810	7.7	1450	95	221	53	821	43	659	43		
19	480	8.8	960	100	226	65	1199	49	535	47		
20	680	7.3	900	72	360	45	695	37	352	44		
21	480	8.6	780	58	221	42	636	37	448	54		
22	670	8.2	1120	62	350	48	726	39	571	52		
23	660	7.9	870	109	146	59	1080	54	415	47		
24	700	7.7	900	40	544	27	245	22	215	40		
25	700	7.8	890	41	612	39	391	23	444	42		
26	890	7	1050	60	298	46	673	37	412	50		
27	450	9.1	970	51	366	36	453	34	559	57		
28	520	8.8	1010	50	279	44	579	32	334	51		

On each Douglas fir stand four regeneration subplots covering a size of 2 x 2 m were established in four directions 10 m from the plot centre (Golser and Hasenauer (1997). On these subplots representative trees by height class and species group were selected to record the tree height and 5-year height increment. Three species-groups (Douglas fir, Other conifers, Other broadleaves) and 4 height classes (1 cm-20 cm; 21 cm-50 cm; 51 cm-100 cm; 101 cm-130 cm) were defined. The group "Other conifers" include mainly Norway spruce, and "Other broadleaves" mainly Common beech. For recording trees in the intermediate layer (ranging from h > 1.3 m to dbh \leq 10 cm), the size of the four subplots was enlarged to 5 m by 5 m. Again the species group, dbh, tree height and height to the life crown base was recorded. More details on the recording of regeneration data can be found in Golser and Hasenauer (1997).

Potential compensatory effects on juvenile tree growth due to edge effected incidence of light (see Golser and Hasenauer 1997) were addressed by measuring the distance in 8 directions from the four subplot centres to the stand edge if the distance was

less than twice the dominant tree height e. g. about 60 m. The humus type was classified according to three categories: mull, mull-behaved decay, decay. A summary of the available data for calibrating regeneration establishment and juvenile tree height growth is shown in Table 2 and Table 3.

Table 2: Summary of the regeneration data, where D is Douglas fir, Co Other conifers, Br Other broadleaves, Re is regeneration (≤ 1.3 m in height), IL is the intermediate layer (> 1.3 m in height and ≤ 10 cm in dbh), dbh_{max} is maximum diameter, konk the competition index according to equation (2), Hum is the humus type, Mull is mull, Mod is decay, MuMo is mull-like decay. "-" indicates that no adult tree was on the plot.

Plot	N_{Re_D}	$N_{\rm IL_D}$	dbh_{max_D}	N _{Re_Co}	N_{IL_Co}	dbh_{max_Co}	N_{Re_Br}	N_{IL_Br}	dbh_{max_Br}	konk	Hum
Nr.	(N/ha)	(N/ha)	(cm)	(N/ha)	(N/ha)	(cm)	(N/ha)	(N/ha)	(cm)		
1	0	0	68	0	0	59	0	0	-	1.5	Mull
2	0	0	69	0	0	-	10625	900	-	3.8	Mull
3	0	0	66	0	0	-	0	200	-	3.7	Mull
4	0	0	29	0	0	44	0	0	-	4.4	Mod
5	0	0	50	0	0	-	24375	0	23	4.6	Mod
6	59357	0	43	0	0	-	4375	0	-	1.9	Mull
7	1250	300	80	0	0	-	0	0	-	1.5	Mull
8	43125	0	52	1250	0	31	0	0	21	6.3	MuMo
9	0	0	43	0	0	-	0	0	-	3.8	Mod
10	6250	0	46	25000	0	-	625	0	-	2.6	MuMo
11	6875	100	73	17500	0	23	30625	500	-	5.5	Mull
12	5000	100	77	6250	300	-	1875	100	-	5.5	Mod
13	0	0	125	0	0	-	0	0	-	3.4	Mull
14	3750	0	96	0	200	64	0	700	-	3.1	Mull
15	1250	500	95	16250	1400	-	0	100	-	5.8	Mod
16	1250	200	99	8125	200	-	625	200	-	3.1	Mod
17	0	0	57	0	0	40	0	0	-	5.3	Mod
18	1875	100	91	11250	2200	-	18750	2800	44	7.5	Mull
19	0	0	91	625	100	-	0	0	-	4.4	Mull
20	37500	0	71	103125	0	-	625	0	-	6.3	MuMo
21	625	0	70	1250	0	44	31250	0	33	3.5	Mod
22	0	0	70	71250	600	59	625	1600	-	10.2	Mod
23	0	0	97	0	0	77	0	100	40	2.4	Mull
24	0	0	43	0	0	-	0	0	-	3.1	Mull
25	0	0	40	0	0		0	0	-	4.8	Mull
26	0	0	69	0	0	39	0	1000	-	4.3	Mull
27	0	0	54	0	200	-	3750	5700	23	4.9	Mull
28	0	0	55	0	0		625	700	-	3.4	Mull

	Dougla	s fir			Other co	Other conifers				Other broadleaves			
N	39				57				44				
Variable	Min	Mean	Max	Sd	Min	Mean	Max	Sd	Min	Mean	Max	Sd	
h _{Rep}	3.5	30.1	125.0	33.9	3.5	40.4	120	32.6	6.0	49.1	127	34.4	
ihobs	6.5	25.7	66.0	14.3	2.5	21.9	56.0	12.4	7	33.4	105	21.6	
ih _{pot}	134	238	295	29.5	216	271	338	30.2	89.7	138	237	47.8	
N_{taller}/m^2	0	0.79	4.0	1.06	0	1.26	4.0	1.24	0	0.64	3	0.84	
CCF	77.1	395	906	205	237	457	906	157	142	433	659	144	
SUMD	0	1.03	5.94	1.32	0	0.71	3.83	1.02	0	0.69	3.83	0.91	

Table 3: Summary of species-specific data for calibrating the 5-year juvenile tree growth.

N Number of representative trees $h_{\text{Rep}}[cm]$ Height of the representative tree

ih_{obs}[cm] Observed 5-year height increment of the representative tree ih_{pot}[cm] Potential 5-year height increment according to SI-curves Na_{aler}/m² Number of trees per m² taller than the subject tree CCF Overstorey crown competition factor (trees > 10cm dbh) SUMD Weighted sum of distances / light-incidence due to edge effect

Sd Standard deviation

4. Analysis and results

4.1 Regeneration model for Douglas fir

4.1.1 Regeneration establishment

We start the calibration by assessing the probability of Douglas fir regeneration establishment (P_{BA}) with a logistic regression:

$$p_{BA} = \frac{1}{1 + e^{-1 \cdot (a \cdot konk + b \cdot dbh_{max} + c_{Hum})}}$$
 (6)

Note that P_{BA} is a binary coded (yes/no) variable. Thus ML (Maximum Likely Hood) procedure is required for deriving the coefficient estimates (Hasenauer and Kindermann, 2006; Monserud and Sterba, 1999; Pretzsch et al., 2002). The estimated coefficients are given in Table 4. Since we cannot assume that on each plot all the established regeneration survives, we compare the results from equation (6) with a random number ranging between 0 and 1. If the random number is higher than the calculated probability, a successful regeneration establishment is assumed otherwise P_{BA} is set equal to zero.

4.1.2 Regeneration Density

n.c.

Once it is decided that regeneration occurs, we can estimate the number of trees by tree species and per m² (N_{BA}) according to equation (7):

$$N_{BA} = e^{(a \cdot konk + b \cdot dbh_{max} + ci_{Hum})} \tag{7}$$

konk is the competition index according to equation (2) dbh_{max} the maximum diameter at breast height for a given tree species, and Hum the humus type, a, b, c are the corresponding parameter estimates. Parameter c has three manifestations, mull, mull-behaved decay, decay. Parameters for Douglas fir are represented in Table 4.

Table 4: Variables and coefficient estimates for the models of probability and density of regeneration of Douglas fir

Variable	coeff	P Dou	N Dou					
konk	a	-0.1825x	0.1288 ^x					
$dbh_{\max, Dou}$	b	-0.0331x	-0.0288x					
Mull	\mathbf{c}_1	n.c.	n.c.					
MuMo	c_2	n.c.	n.c.					
Mod	c ₃	n.c.	n.c.					
n		28	28					
NULL dev		38.8	52.0					
Res dev		28.1	32.0					
konk	* $\alpha = 0.001$ ** $\alpha = 0.01$ Measure of concurred	nce						
Mull, Mod, MuMo coeff	Mull is mull, Mod is coefficient	Mull is mull, Mod is decay, MuMo is mull-like decay coefficient						

Number of stands NULL dev NULL deviance Res dev Residual deviance P Dou Regeneration probability of Douglas fir N Dou Regeneration density of Douglas fir Not certain at $\alpha = 0.05$ and used for the regeneration model. Not certain at $\alpha = 0.05$ and not used for the regeneration model.

4.1.3 Juvenile tree growth

Next we derived coefficients for calculating juvenile tree height growth according to equation (4). We also do this for the species groups "Other coniferous" and "Other broadleaves" so that we can compare the juvenile tree height growth of Douglas fir with the other species groups on our forest plots. The estimated coefficients follow a non-linear regression using the statistical software R (Team, 2014). The results are given in Table 5.

Table 5: Variables and coefficient estimates for the tree juvenile height increment model.

Variable	Coeff	Douglas fir	Other conifers	Other broadleaves
CCF	a	0.05481***	0.02831***	0.01474**
N_{Taller}	b	0.12137	1.36709	0.97403
SUMD	c	-0.04093***	-0.00556	-0.02883
n		39	57	44
Se		0.167	0.128	0.235

significant with *** $\alpha = 0.001$ ** $\alpha = 0.01$ * $\alpha = 0.05$

CCF Crown Competition Factor

N_{Taller} Number of trees taller than the subject tree

SUMD Sum of Distances as measure for edge effected incidence of light

n Number of observations

Se Standard error (m)

We can now assess the development of the relationship between the ratio predicted/potential 5-year height increment versus CCF (crown competition). SUMD and N_{Taller} are kept constant by inserting the mean values of each tree species. The results in Figure 1 show Douglas fir and the species groupings "Other broadleaves" and "Other conifers" based on data from this study and Douglas fir compared to the results of Common beech and Norway spruce obtaining the parameters from Hasenauer and Kindermann (2006).

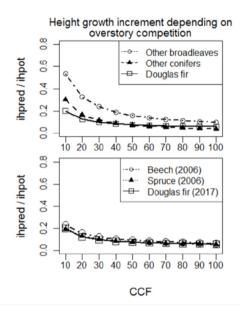


Figure 1: Increase in the relative 5-year height increment of juvenile Douglas fir trees and species groups versus overstory competition expressed by the CCF (Crown Competition Factor). The figure on top depicts Douglas fir and the groups Other Broadleaves and Other Conifers based on coefficients calculated in this study and bottom graph shows Douglas fir with parameters from this study and beech and spruce with parameters from Hasenauer and Kindermann (2006)

Next the influence of edge effected incidence of light on juvenile tree height growth expressed by the factor *SUMD* is shown (see Figure 2) by keeping *CCF* and N_{Taller} at a constant level using the mean values by tree species. As shown in Figure 2 the influence of edge effected incident of light for Douglas fir declines to almost zero within 60 m.

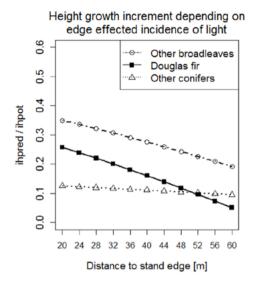


Figure 2: Development of the height-growth rate of juvenile trees versus edge effected incidence of light expressed by the index SUMD. The results show the compensatory effects. Apparently from an additional light supply due to edge effected incidence of light the group "Other broadleaves" benefits most.

4.2 Model evaluation

For assessing the predictive power of our regeneration probability model (see equation 6 and Table 4) we compare the estimated probability of regeneration establishment versus the observed regeneration data from our 28 Douglas fir stands. Since the final decision if regeneration establishment occurs is a combination of a prediction (see equation 6) and a random number, different prediction runs produce slightly different results. Therefore we simulate 20 prediction runs each for all 28 regeneration plots and calculate the ratio of correctly predicted stands. For example, if for a given stand regeneration is predicted and was also evident from the recorded data, the prediction result is classified as correct. The calculated mean percentage of correct predictions was 67.3%. That means 19 of the 28 forest stands were correctly classified.

The evaluation of regeneration density predictions follows a correlation between predicted and recorded densities. After applying equation (7) we perform 20 prediction runs, each comprising all 28 stands. After each prediction run we plot the predicted numbers of regenerated trees versus the recorded numbers to calculate a correlation coefficient. The mean of the 20 correlations coefficients was 0.27.

The juvenile tree height increment model was evaluated by calculating the differen-

ces between predicted 5-year height versus recorded 5-year increment so that the confidence (CI), tolerance (TI), and prediction interval (PI) (Reynolds, 1984) can be calculated:

$$CI = \overline{D} \pm \frac{S_D}{\sqrt{n}} \bullet t_{1 - \frac{\alpha}{2}, n - 1}$$
 (8)

$$PI = \overline{D} \pm S_D \bullet \sqrt{1 + \frac{1}{n}} \bullet t_{1 - \frac{\alpha}{2}, n - 1}$$
 (9)

$$TI = \overline{D} \pm S_D \bullet g_{1-\gamma,n,1-\alpha} \tag{10}$$

with \overline{D} as mean of differences between predicted and observed values, S_D the standard deviation, n the number of observations, t the value from t-distribution, $1-\alpha/2$ the quantile of the t-distribution, n-1 the degrees of freedom and g the tolerance factor. Both t-value as well as g-value can be extracted from Kokoska and Nevison (1989). The results are given in Table 6.

Table 6: Mean difference between predicted and observed juvenile height increment by species and height class. The confidence interval (CI, α =0,05) shows the mean of the differences between predicted and observed values, the prediction interval (PI, α =0,05) gives the variation range of the differences between predicted and observed increment, the tolerance interval (TI, γ =0,95 und α =0,05) indicates the error to be expected by applying the model repeatedly (Reynolds, 1984).

Species	Height Class	N	$\overline{ih}_{obs}[cm]$	$\overline{D_i}[cm]$	$S_D[cm]$	CI [cm]	PI [cm]	TI [cm]
Douglas fir	1	24	17.7	3.4	12.0	-1.8 to 8.6	-21.9 to 28.8	-32.2 to 39.1
	2	6	28.0	-1.7	9.4	-12.5 to 9.1	-28.2 to 24.7	-20.0 to 16.5
	3+4	9	45.5	-23.7	11.2	-32.8 to -14	.6 -51.0 to 3.5	-44.1 to 3.4
Other	1	19	13.7	7.3	8.2	3.2 to 11.4	-14.4 to 25.1	-16.9 to 31.4
Conifers	2	21	19.7	0.0	6.1	-2.9 to 2.7	-13.1 to 12.9	-16.5 to 16.3
	3	12	32.8	-10.4	11.2	-17.8 to -3.0	-36.2 to 15.4	-39.3 to 18.5
	4	5	36.8	-14.1	23.5	-46.7 to 18.5	5 -87.1 to 58.8	-53.4 to 25.1
Other	1	12	21.6	5.5	7.1	-0.8 to 10.2	-10.8 to 21.8	-13.3 to 24.2
Broadleaves	2	14	37.6	-12.0	28.9	-29.3 to 5.3	-76.7 to 52.8	-86.4 to 62.6
	3	14	39.5	-10.1	26.0	-25.7 to 5.4	-68.3 to 48.1	-70.6 to 50.4
	4	4	32.4	12.2	34.5	-51.2 to 75.0	6 -115 to 139	-27.5 to 51.8
N	Number of	f representati	ve trees		C	I	Confidence interval (α=0,05)	
\overline{ih}_{obs}	Mean obse	rved 5-year	height increment		PI		Prediction interval (α=0,05)	
$\overline{D_l}$	Mean diffe	erence			TI		Tolerance interval (y=0,95 and	α=0,05)
S_D	Standard d	leviation						

4.3 Model integration in MOSES and analysis of invasiveness

The final step of our work is the integration of the Douglas fir regeneration equations within the tree growth model MOSES to perform simulations according to common forest management scenarios. We did this for several Douglas fir stands and demonstrate here as an example, the Douglas fir stand No 18 of our data (see Table 1). The forest has a stand age 95 years, and the potential natural vegetation is *Asperulo-Fagetum*. The stand covers three tree species, Douglas fir with a relative base are of 67%, Common beech 19%, and Norway spruce with a 14% share of the total base area. The mean diameter of Douglas fir trees is 52 cm, Common beech 7 cm, and Norway spruce 7 cm. Thus the stand comprises an overstory layer dominated by Douglas fir, intermediate and regeneration layer covering all three species. The tree numbers in the understory (see Table 2) shows that Common beech is dominant species followed by Norway spruce and Douglas fir. We simulate the stand for 100 years assuming two management scenarios:

Variant A assumes in the first 5-year period a removal of 50% of the stem volume for Douglas fir, to initiate regeneration, in the second 5-year period 40% of the stem number for Common beech is removed and in the fourth 5-year period the remaining 50% of the volume of Douglas fir is assumed to be harvested.

Variant B assumes the same measures, with the only exception that in second 5-year growth period the stem reduction for Common beech is 80% versus 40% in Variant A.

The results of these simulation runs are depicted in Figure 3.

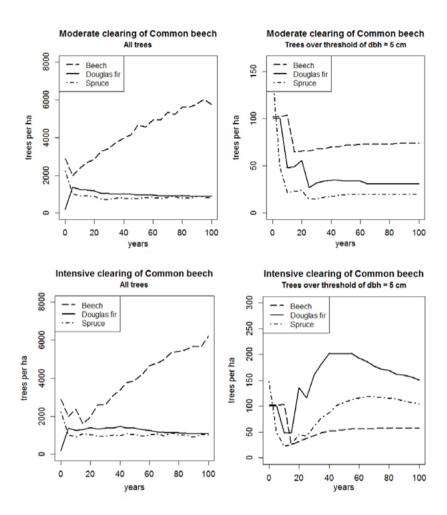


Figure 3: Simulation result with MOSES after implementing the regeneration model for Douglas fir. Stand No 18 is used, the simulation length are 20 5-year growth periods (=100 years). The left plots show the stand development considering all trees. The plots on the right side show the results only for trees with a dbh larger 5 cm. The plots in the top line represent moderate clearing of Common beech in the second growth period (removal of 40% of the stem number) and on the bottom we show results for intensive clearing of Common beech (removal of 80% of the stem number).

5. Discussion

The probability of regeneration within a 5-year growth period (equation 6) depends mainly on the overstory competition and the largest tree by species.

The calibrated model for tree height increment of juvenile Douglas fir (equation 4) strongly depends on overstory competition expressed by the crown competition factor CCF and edge effected incidence of light expressed by *SUMD*. The third parameter, N_{Taller} which addresses the competition within the regeneration exhibited no significant influence (see Table 5).

The residual analysis showed that for 8 of 11 height classes the confidence interval CI is within 5% probability range and shows no bias, PI the prediction interval and TI the tolerance interval exhibited no significant differences for all tested height classes and species groups (see Table 6). The evaluation of the equations (6) and (7) reveals that for the predictions of regeneration establishment and tree density reliable results can be expected.

The consistent model behaviour in future application is also demonstrated by the analyses reflecting from Figures 1 to 3. Figure 1 shows the 5-year height increment of the three species in dependency of *CCF*. Both images of Figure 1 (image above and image below) suggest that even if Douglas fir benefits from an additional availability of light, Common beech apparently profits more and grows faster. The superiority of Other broadleaves is striking in Figure 1, picture above. But it is remarkable also in the Figure 1, picture below, where Douglas fir is compared with Common beech and Norway spruce from the study of Hasenauer and Kindermann (2006). Thus Figure 1 clarifies that on the investigated plots beech is the main competitor to Douglas fir, and it's growing behavior is remarkably in advantage compared to Douglas fir. This suggests that without supportive interventions Douglas fir will certainly not be able to maintain the position of principal tree species in the long run, as it is the case at present on all the 28 plots.

The same result is shown in Figure 2, where the height growth increment by species depends on *SUMD*, the compensation factor for edge effected incidence of light. At a given light level Douglas fir exhibits lower height growth rates versus Common beech, which indicates that Common beech outcompetes Douglas fir.

Considering the outcome of the performed simulations in MOSES (Figure 3) we can observe that in variant A (Figure 3, above), which assumes a rather moderate reduction of Common beech trees in the juvenile phase (removal of 40% of the stem number), the main competitor of Douglas fir, i.e. Common beech is superior in both, the regeneration layer (Figure 3, above, left hand) as well as the top layer (Figure 3, above, right hand). In variant B (Figure 3, below), which involves a much stronger removal of Common beech at the juvenile stage (removal of 80% of the stem number), Common

beech is still superior versus Douglas fir (Figure 3 below, left hand). In the top layer Douglas fir is clearly the main tree species at the end of the rotation period (Figure 3 below, right hand).

6. Conclusion

The calibrated equations for predicting regeneration establishment, tree density and juvenile Douglas fir tree height growth reveals unbiased and consistent results. It can be easily implemented in the tree growth simulator MOSES and in combination with the Douglas fir growth functions of the overstory trees it provides a simple but easy to use tool for forest management scenario analysis. The study also demonstrates that the non-native Douglas fir regenerates well naturally but the juvenile Douglas fir trees experience strong competition by the native tree species, mainly Common beech which gradually displaces Douglas fir. This suggests that Douglas fir does not show any invasive behavior on the investigated stands and, if not promoted by forest management, it will be displaced by natural succession of native tree species such as Common beech.

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References

- Biber, P., Herling, H., 2002. Modellierung der Verjünungsdynamik als Bestandteil von einzelbaumorientierten Waldwachstumssimulatoren. Sekt. Ertragskd. DVFF, Schwarz. 194–216.
- BMEL, 2014. Der Wald in Deutschland Ausgewählte Ergebnisse der dritten Bundeswaldinventur. Bundesministerium für Ernährung und Landwirtschaft (BMEL, Hrsg.), Berlin.
- Eckenwalder, J.E., 2009. Conifers of the world: the complete reference. Timber Press.
- Eckmüllner, O., 2015. Ertragstafel Douglasie für systematische oder zufällige Entnahme. St. Pölten.
- Eilmann, B., Rigling, A., 2012. Tree-growth analyses to estimate tree species' drought tolerance. Tree Physiol. 32, 178–187. doi:10.1093/treephys/tps004
- Ferguson, D.E., Carlson, C.E., 1993. Predicting regeneration establishment with the Pro-

- gnosis Model. Res. Pap. INT.
- Ferguson, D.E., Stage, A.R., Boyd, R.J., 1986. Predicting regeneration in the grand fir-cedar-hemlock ecosystem of the northern Rocky Mountains. For. Sci. 32, a0001-z0001.
- Gabler, K., Schadauer, K., 2008. Methods of the Austrian Forest Inventory 2000/02.
- Golser, M., Hasenauer, H., 1997. Predicting juvenile tree height growth in uneven-aged mixed species standes in Austria. For. Ecol. Manage. 97, 133–146.
- Hasenauer, H., 2006. Concepts within tree growth modeling, in: Sustainable Forest Management. Springer Berlin Heidelberg, pp. 3–17.
- Hasenauer, H., 1997. Dimensional relationships of open-grown trees in Austria. For. Ecol. Manage. 96, 197–206.
- Hasenauer, H., 1994. Ein Einzelbaumwachstumssimulator für ungleichaltrige Fichten-Kiefern- und Buchen-Fichtemnischbestände. Forstl. Schriftenreihe, Univ. f. Bodenkultur, Wien. Österr. Gesellschaft für Waldökosystemforschung und experimentelle Baumforschung an der Univ. f. Bod.
- Hasenauer, H., Kindermann, G., 2006. Modeling regeneration in even and uneven-aged mixed species forests, in: Sustainable Forest Management. Springer, pp. 167–193.
- Hintsteiner, W. J., van Loo, M., Neophytou, C., Schueler, S., Hasenauer, H., 2018. The geographic origin of old Douglas fir stands growing in Central Europe. Submitt. to For. Ecol. Manag.
- Hynynen, J., Ojansuu, R., Hökkä, H., Siipilehto, J., Salminen, H., Haapala, P., 2002. Models for predicting stand development in MELA system. Metsäntutkimuslaitos.
- Kindermann, G. E., 2004. Wachstumssimulation in Mischbeständen. Universität für Bodenkultur Wien.
- Kindermann, G. E., Hasenauer, H., 2005. Zusammenstellung der Oberhöhenfunktionen für die wichtigsten Baumarten in Österreich. Austrian J. For. Sci. 122, 163–184.
- Klopf, M., 2014. Moses: A single tree growth simulator for forest management planning. Doctoral thesis, Universität für Bodenkultur, Wien.
- Köble, R., Seufert, G., 2001. Novel maps for forest tree species in Europe, in: "Proceedings of the 8th European Symposium on the Physico-Chemical Behaviour of Air Pollutants": a Changing Atmosphere. pp. 17–20.
- Kokoska, S., Nevison, C., 1989. Critical values for the studentized range distribution, in: Statistical Tables and Formulae. Springer, pp. 64–66.
- Krajicek, J.E., Brinkman, K.A., Gingrich, S., 1961. Crown competition. A measure of density. For. Sci 7, 35–42.
- Lavender, D.P., Hermann, R.K., 2014. Douglas-fir: The Genus Pseudotsuga. Corvallis, OR: Forest Research Publications Office, Oregon State University.
- Mayer, F., 2014. Ein Einzelbaummodell für Douglasie (Pseudotsuga menziesii) für den Waldwachstumssimulator MOSES. Universität für Bodenkultur Wien.
- Miina, J., Saksa, T., 2006. Predicting regeneration establishment in Norway spruce plantations using a multivariate multilevel model. New For. 32, 265–283.
- Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. For. Ecol. Manage. 113, 109–123.

- ÖWI [WWW Document], 2016. URL http://bfw.ac.at/rz/wi.auswahl (accessed 10.13.16).
- Peterson, D.L., 1985. Crown scorch volume and scorch height: estimates of postfire tree condition. Can. J. For. Res. 15, 596–598.
- Pharis, R.P., Ferrell, W.K., 1966. Differences in drought resistance between coastal and inland sources of Douglas fir. Can. J. Bot. 44, 1651–1659.
- Pollanschütz, J., 1975. Erste ertragskundliche und wirtschaftliche Ergebnisse des Fichten-Pflanzweiteversuches "Hauersteig." na.
- Pretzsch, H., Biber, P., Dursky, J., 2002. The single tree-based stand simulator SILVA: construction, application and evaluation. For. Ecol. Manage. 162, 3–21.
- Reynolds, M.R., 1984. Estimating the error in model predictions. For. Sci. 30, 454–469.
- Schweiger, J., Sterba, H., 1997. A model describing natural regeneration recruitment of Norway spruce (*Picea abies* (L.) Karst.) in Austria. For. Ecol. Manage. 97, 107–118.
- Solomon, D.S., Leak, W.B., 2002. Modeling the regeneration of northern hardwoods with FOREGEN.
- Thurnher, C., Klopf, M., Hasenauer, H., 2017. MOSES A tree growth simulator for modelling stand response in Central Europe. Ecol. Modell. 352, 58–76.